or to disprove, and the Antarctic holds for us innumerable problems of which we can foresee neither statement nor solution, as well as the solution of those that we can already in some measure foresee.

"On the Zoological Evidence for the Connection of Lake Tanganyika with the Sea." By J. E. S. Moore, A.R.C.S. Communicated by Professor Lankester, F.R.S. Received January 12,—Read January 27, 1898.

(From the Huxley Research Laboratory, Royal College of Science, London.)

Before 1896, when I had the opportunity of studying the fauna of Lake Tanganyika on the spot, it was known that there existed in the so-called Sea of Ujiji, one animal, the affinities of which are undoubtedly marine. This was the medusa *Limnocnida*, which Dr. Boehm saw as he crossed the lake in 1883.

It was known further that the jelly-fish was associated in Tanganyika with a number of strange molluscan forms, for the empty shells of what appeared to be some six entirely new genera of gasteropods, had been brought home by Captain Speke, Joseph Thomson, and Mr. Hore. As the animals contained in these shells have not hitherto been known, their classification by the conchologists with existing fresh-water types has always appeared extremely doubtful, and from the first Mr. Edgar Smith, who described the greater number of these forms, has held the opinion that they might eventually turn out to have the same oceanic characters as the jelly-fish.

It was therefore one of the objects of my recent expedition to obtain material for the complete determination of these molluscous types, and especially to ascertain if there were any other marine organisms in the lake. The results of this attempt have been to show:—

I. That to the six genera of quasi-marine gasteropods, the shells of which were known, viz., *Typhobia*, *Nassopsis*, *Limnotrochus*, *Syrnolopsis*, the so-called *Lithoglyphus*, and *Paramelania*, there are now to be added at least two, entirely new generic forms, for which I propose the names* *Bathanalia* and *Bythoceras* (figs. 1 and 2). We have therefore now representing the quasi-marine molluscs of Tanganyika eight genera of gasteropods, and to these should probably be added among the Lamellibranchiata the so-called *Unio Burtoni* and one of the Tanganyika Spathas.†

* Diagnoses of these new genera will be found in papers now in the hands of the Editor of the 'Quart. Journ. Micr. Sci.'

† Complete accounts of the anatomy of all these Halolimnic genera will shortly appear in the 'Quart. Journ. Micr. Sci.'

II. That among the invertebrate population of Tanganyika there are a large number of widely separated animal types, all of which

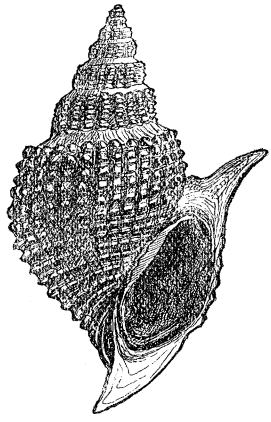

Fig. 1.—Shell of *Bythoceras iridescens* obtained living near Sumbu, Tanganyika, at a depth of 680 ft.

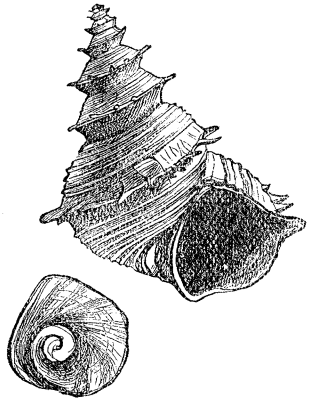

Fig. 2.—Shell of *Bathanalia Howesii*, obtained near Mleroes, Tanganyika, at a depth of 950 ft.

possess the same quasi-marine affinities. Thus I found that among the Crustacea there are two forms of prawns and one deep-water crab. Among the Hydrozoa the already known medusa *Limnocnida*. Among Porifera one deep-water sponge; and lastly there are several forms of *Peridinea* and *Condylostoma* among the Protozoa. A large proportion of these organisms are exceedingly peculiar; but others such as the two prawns, the deep-water crabs and sponge, and pos-

sibly the pelagic Protozoa, are much more nearly related to the similar marine organisms which have repeatedly contaminated the fresh waters of the world elsewhere. It should, however, be clearly understood that even these apparently more normal types have not been found in Nyassa, Shirwa, or Kela, nor have they been recorded from any of the Great Lakes further north. Therefore, although they are less peculiar than their associates in Tanganyika, they probably belong to the same quasi-marine, or what I shall in future call the *Halolimnic* group.

The results of a systematic survey which was made of the geographical and bathymetric distribution of the aquatic molluscs throughout the wide area over which the expedition had to pass have demonstrated in the most conclusive manner the complete duality of the Tanganyika fauna as a whole.* In Nyassa, Shirwa, Kela, and several minor lakes, taken together, all of which I visited and dredged, there have been found the following molluscous types:—*Unio*, *Spatha*, *Corbicula*, *Iridina*, *Limnæa*, *Isodora*, *Physopsis*, *Planorbis*, *Ancylus*, *Ampullaria*, *Lanistes*, *Vivipara*, *Cleopatra*, *Bithynia*, and *Melania*.

Not all of these fifteen genera which are now found living in Nyassa are present in the smaller lakes. In the Shirwa they are reduced to five, and in Kela they are only three. The full Nyassan series has, however, been recorded from the Victoria Nyanza, and in this more northern group of lakes there is again seen the curious reduction in the number of genera as we pass from the greater lakes to the less. From these facts of distribution it is apparent that the genera of molluscs, which occur in the African fresh waters, are very constant over an immense area of ground. There can indeed be little doubt that the genera found in Nyassa characterise and constitute the type of the truly African fresh-water fauna as a whole.

The fauna of Tanganyika appears therefore to form a striking contrast to this rule of uniformity in type which characterises the fauna of all the other lakes. Such divergence is, however, in one sense more illusory than real. All the Nyassa or Victoria Nyanza genera are found living in Tanganyika, and the fauna of this lake does not differ from the faunas of the others in kind or as a whole. It differs from them merely in there being here added to the normal series a number of molluscs which are not found elsewhere. To this superadded list, however, there attaches a unique interest, as it is entirely composed of those ten genera of gasteropods and lamellibranchs which were instanced as possessing the same marine appearance as the jelly-fish and prawns.

The strange geographical isolation of the halolimnic molluscs which

* The full details of my observations on the distribution of the Halolimnic molluscs are now in the hands of the Editor of the 'Quart. Journ. Micr. Sci.'

these facts disclose is also true and characteristic of all the other halolimnic animals I have named. It is thus rendered evident that the entire halolimnic fauna as it exists in Tanganyika now is something completely distinct from and superadded to the normal African lake fauna as a whole. This fact is of the utmost import when we attempt to ascertain from what source the halolimnic animals have sprung.

The isolation of these animals shows conclusively that they cannot have arisen, so to speak, *de novo* in Tanganyika through the effect of the conditions under which they live, for if this were so there would have arisen similar halolimnic animals under the apparently similar conditions which exist elsewhere. For the same reason they cannot be regarded as the surviving representatives of an older fresh-water stock, since were this the case we should have to believe that this old stock had been destroyed in every African lake but one. Nyassa, moreover, appears to have been a fresh-water lake longer than Tanganyika, yet in the Post-pleistocene deposits which occur along its shores no halolimnic fossils have been found.

Now it is perhaps conceivable that prawns, which are active vigorous organisms, could by great exertions have made their way up the numerous falls along the single effluent of Tanganyika from the sea in recent times, for they have certainly thus entered many lakes already known. But with respect to the remaining halolimnic organisms, there is a singular feature common to them all which effectually precludes any possibility of this. All these animals are incapable of being directly associated with any *living* oceanic species. This fact alone demonstrates conclusively that the halolimnic fauna, wherever it came from, must be old. It has either had time to modify into its present condition from forms which are already known, or, what is more probable, it has more or less adhered to the characters of the older types from which it sprang. Delicate organisms, such as the Medusa, could not have found their way up the effluent as it now exists: it is barely conceivable that they can have been carried overland, while it is altogether out of the question to suppose that either of these processes could account for the presence of the halolimnic molluscs in the lake, as these are almost exclusively deep water forms. The genus *Typhobia* and the genus *Bathanalia* are generally beyond the hundred fathom line. *Limnotrochus* and *Syrnolopsis* are never found in less than 200 feet, and they occur up to 700 feet. The morphology of these molluscs is therefore of the first importance in determining the nature of the halolimnic group, for if the affinities of these organisms have been misinterpreted, and if in reality it can be shown that they have been derived from ancient oceanic types, they must have made their way into Tanganyika from the sea under widely different conditions from those which now exist; in fact, the

proof of their oceanic character will more or less necessitate the idea that the Tanganyika region of to-day must have approximated in character to an arm of the deep and open sea in ancient times.

During my late expedition I was able to obtain sufficient material for the complete morphological investigation of all the halolimnic molluscs, the shells only of which have hitherto been known, as well as for the two new genera *Bathanalia* and *Bathoceras* represented in figs. 1 and 2, and as I have worked over in detail a considerable number of these forms I am now in a position to state definitely what they really are. In 1857 S. P. Woodward, when describing the shells of the so-called *Lithoglyphus* of Tanganyika, which had been obtained by Speke, observed "the univalve . . . . so much resembles a *Nerita* or *Calyptræa* that it would be taken for a sea shell if its history were not so well authenticated," and similar reflections were made by other observers when describing the shells more recently obtained by Captain Hore.

But possibly owing to the weight then attached to Murchison's geological speculations respecting the African interior, undoubtedly to the fact that the Tanganyika jelly-fish was not then known, and also because the fresh-water habitat of these molluscs was indisputable, the idea of their marine origin which was thus distinctly before the minds of older zoologists subsequently became entirely obscured. The shell of Typhobia was hesitatingly classed by Smith in 1881, and more definitely by Fischer in 1887, with the Melanidæ* as a subsection of that group. The shells of the Paramelanias were regarded as nearly related to the same, while the really unique so-called *Lithoglyphus* of Tanganyika was equally misplaced. The mere fact of the jelly-fish being, as I ascertained, associated with other marine organisms in Tanganyika would throw suspicion on these purely conchological determinations, and the actual anatomical character of the halolimnic molluscs entirely confirms this view. The Typhobias are utterly unlike any *Melania* the anatomy of which is known. These gasteropods in the character of their radulæ and their alimentary canals, in the presence of a crystalline style and an anterior stomachic cœcum, in the possession of a well-developed posterior and anterior syphon, in the form of the gills and osphradium, in the position of the anal, genital, and renal apertures, as well as in the gross details of their reproductive apparatus, most closely approximate to *Strombus* and *Pteroceras*. The same inference may be gathered from the longi-commissurate character of the nervous system, while in the absence of a right pallial anastomosis, as well as in the form of the subintestinal ganglionic

* In 1881 Smith became acquainted with the operculum of *Typhobia*, which seemed to confirm this opinion, but it is evident he doubted its correctness from statements on the same page. ('Zool. Soc. Proc.,' 1881, p. 298.)

trunk, the Typhobias undoubtedly approximate to the Solaridæ and possibly to the Scalarids. In fact, the structural *tout ensemble* of the Typhobias leaves little room for question that these gasteropods must be regarded as forms closely similar to a Pteroceras with a non-specialised foot.

What is true of the Typhobias is also true of the allied genus *Bathanalia*, except that this form is in some respects more primitive, and is certainly less specialised in its shell. The so-called *Lithoglyphus zonatus*, *L. neritinoides*, and *L. rufofilosus* are seen at once, when anatomically examined, to have been perhaps even more completely misplaced than the Typhobias. In the characters of their radulæ and alimentary canals they approximate to the *Planaxidæ*,* while in the possession of an anterior stomachic cœcum and style, they show undoubted affinity to some members of the Strombidæ. In the character of their nervous system they are undoubtedly akin to the marine Zygoneurous *Cerithia* on the one hand and the longi-commissurate *Struthiolariidæ* on the other. But the most remarkable anatomical feature which these forms possess is the existence in the female of an enormous epidermal invagination of the body wall beneath the eye (fig. 3), into which the embryos descend from the female genital aperture along a deep groove, and I have now complete evidence for regarding this groove, which is present in both sexes as truly homologous with the similar genital grooves possessed by the *Opisthobranchs*. The affinities of the new genera *Bythoceras*, *Paramelania*, and *Nassopsis*, are much more difficult to determine, but there is no doubt that in the curious condition of their nerves and in the general features of their anatomy they are extremely primitive. The whole nervous system of these forms, in the forwardly elongated character of the pedal ganglia and in the relation and characters of the cerebral and pleural ganglia and their connectives, actually approximate to that of a Cyclophorus. In other respects it resembles that of *Triton*.

Lastly, the one entire *Limnotrochus* which I possess seems to be nearly akin to the Paramelanian group, but the anatomy of this form will require more fully working out by sections than has yet been done.

Thus, although I am not yet able to give a complete statement of the character of all the halolimnic molluscs known, enough anatomical work has now been done for this preliminary communication to indicate clearly what will be the entire result of the investigation. It has been seen that the theory of the marine origin of the

* It is remarkable that representatives of this family abound in the Indian Ocean and on the East African coast, the so-called *Lithoglyphus* of Tanganyika affording one among many instances of similarity between the molluscan fauna of Tanganyika and that of the Indian Ocean.

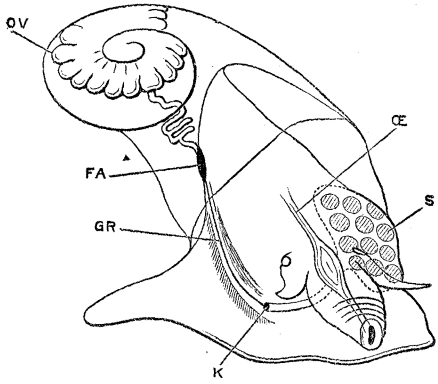

FIG. 3.—Semidiagrammatic representation of the reproductive apparatus in the female of the so-called *Lithoglyphus rufofilosus*. OV, Female genital gland. FA, Opening of oviduct. GR, Genital groove. K, Opening of brood pouch. S, Ova contained in brood pouch. Œ, Œsophagus.

halolimnic fauna of Lake Tanganyika is entirely supported both by the facts of distribution and by those of the morphology of the individual halolimnic forms. Like the medusa, the halolimnic gasteropods combine the characters of several *modern* marine types, and so they cannot by any possibility be regarded as the forerunners of the modern fresh-water stocks.* Consequently, the only way in which their existence in Tanganyika can be accounted for is through the supposition that this region was, as Thomson supposed, at some time in open connexion either on the east, west, or north, with a deep arm of the sea.

Such a conception is, however, in the most uncompromising conflict with the views respecting the permanence of the African terrestrial conditions which were advanced by Sir Roderic Murchison in 1852,† and which have been more recently and so ably advocated by Dr. Gregory in 1896.‡ Nevertheless, the theory of the marine

* It is certain from their anatomical characters that some of the halolimnic molluscs (the Typhobias) originated from marine ancestors later than Cretaceous times, for they possess the characters of genera such as *Strombus* and *Pteroceras*, *i.e.*, genera that are Post-cretaceous and marine. Of the latter of these genera M. Fischer indeed remarks: "L'existence de ce genre à l'état fossile paraît douteuse" ('Manuel de Conchyliologie et Paléontologie Conchyliologique,' p. 671).

† 'Roy. Geogr. Soc. Journ.,' vol. 24, 1864, pp. clxxv—clxxviii.

‡ In his work, 'The Great Rift Valley,' p. 214, Gregory restates the geological position as follows:—"That part of Murchison's theory, which affirms that Central Africa has never been below the level of the sea, is still in harmony with the known facts, for no deposits of marine origin have as yet been found in the interior."

origin of the halolimnic fauna is now supported by an accumulating mass of the strongest kind of zoological evidence it is possible to obtain, while the above geological speculations to which it is diametrically opposed are based at best merely on the continued absence of all definite information respecting the past geological history of the "far interior" of any sort or kind.

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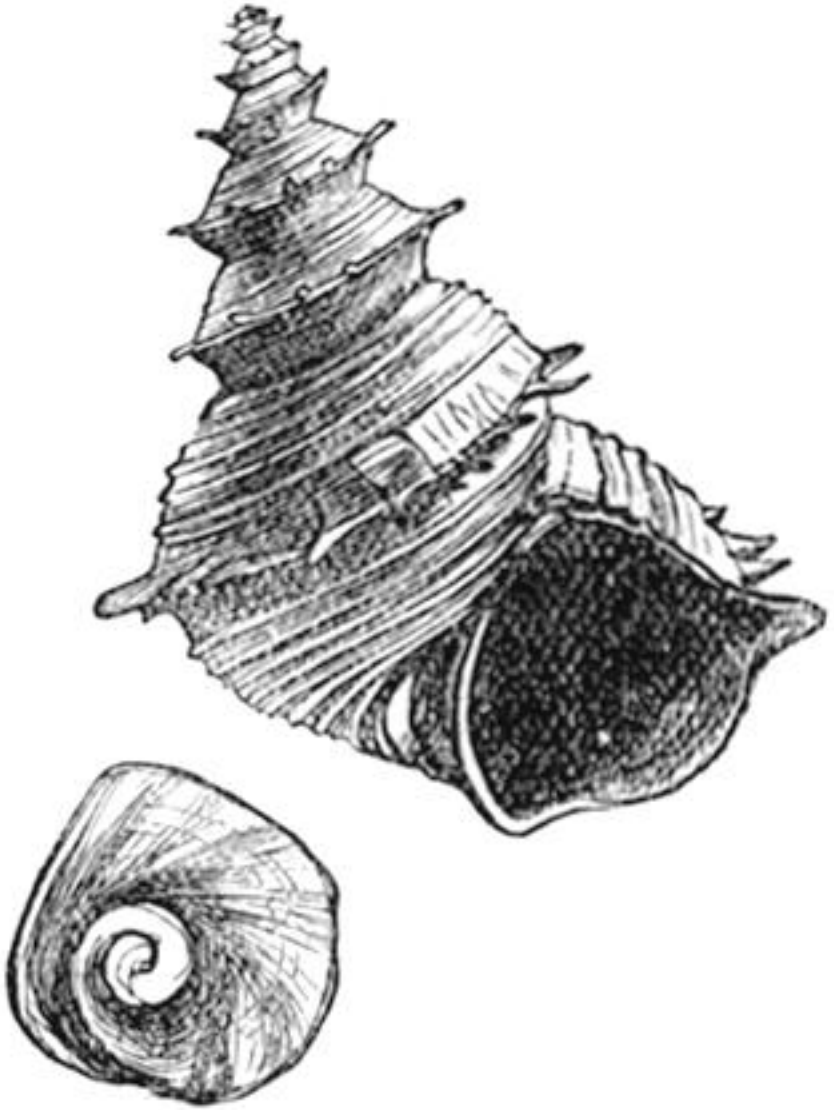

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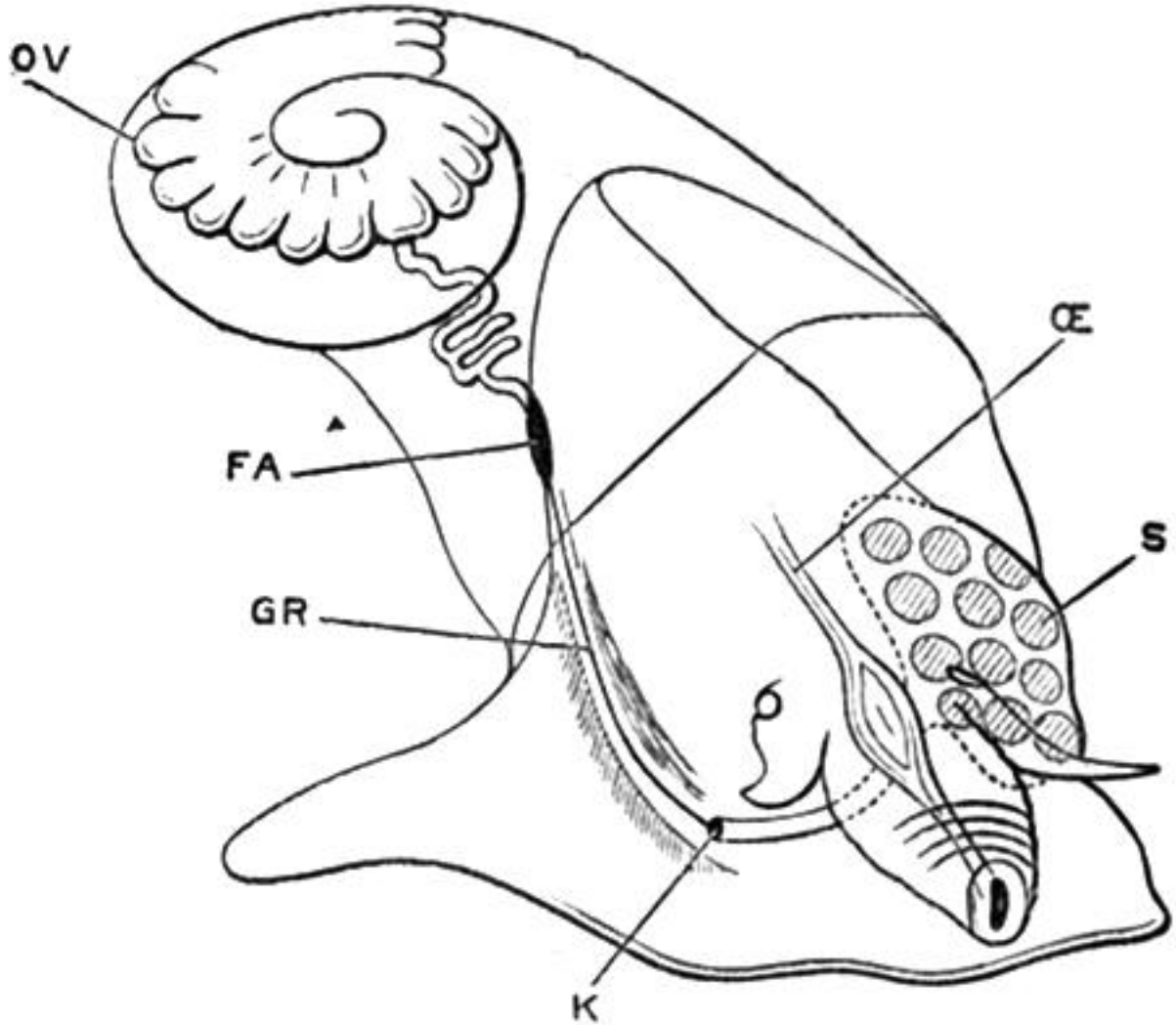

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